The hilltopping mating system of the duskywing skipper *Erynnis tristis* (Lepidoptera: Hesperiidae)

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Abstract. Males of *Erynnis tristis* (Boisduval, 1852) perch at selected locations on a hilltop in central Arizona where they wait for the arrival of receptive females. They leave their perches to engage rival males in chases and, occasionally, in more elaborate spinning, descending flights in which one male appears to force his opponent down toward the ground. This latter behavior has not been previously recorded for *E. tristis* although it is convergent with that of a territorial hilltopping tachinid fly found at the same location. The nature of male-male interactions and the tendency of at least some individual butterflies to remain for some time at a particular perch, or small set of nearby perches, is consistent with male hilltopping territoriality, which has been reported for *E. tristis* at other locations. Although some males do return to the peaktop over periods of as much as three weeks, they do not exhibit fidelity to a particular territory unlike males of many other hilltopping insects at the same location. Moreover, they also differ from most hilltopping insects at this location in frequently choosing to perch in places other than on plants growing on the highest points of the ridge.

Key words: Erynnis, hilltopping, mating system, site fidelity, territoriality.

Introduction

Although the mating systems of a considerable number of butterflies are now known (Thornhill & Alcock, 1983; Dennis & Shreeve, 1988; Rutowski, 1991), skippers (Hesperiidae) remain relatively little studied, but see Shields (1967), Scott (1973), Shapiro (1977), Pivnick & McNeil (1985), Alcock (1988), and Ravenscroft (1994). One mating system that has been well documented for a few hesperiids is hilltopping in which males go to conspicuous landmarks where they wait for receptive females to arrive (e.g., Shields, 1967; Skevington, 2008). Among the hilltopping species is the duskywing skipper *Erynnis tristis* (Boisduval, 1852) (Shields, 1967; Bailowitz & Brock, 1991). Shields (1967) documented that males of this species defend

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territories on hilltops in California and that females visit these sites to mate. This paper describes the natural history of *E. tristis* at an Arizonan hilltop. The data presented here are compared with those collected by Shields (1967). In addition, the mating system of *E. tristis* is contrasted with that of other hilltopping insect species with which the skipper co-exists in central Arizona.

METHODS

The main study of *Erynnis tristis* began on February 24 and ended a month later on March 24, 2009. This work was stimulated by casual observations and occasional records made over the preceding three years at Usery Mountain, north of Mesa, AZ. The study site was a peaktop (elevation about 900 m) in Upland Sonoran Desert habitat (33° 30′ 08″ N and 111° 38′ 30.4″ W) used by many species of insects as a mate rendezvous location (Alcock, 1987; Alcock & Dodson, 2008).

During the month long study in 2009, the peak was visited for between 1.5 and 3 hr on 16 days. On these days, *E. tristis* was found perching on plants along a portion of an undulating hilltop 275 m in length. This section of the ridge was censused several times by an observer during each visit to the peak. A record was kept of the plants occupied by the butterflies.

In addition, during the month, 38 butterflies were captured in an insect net, marked distinctively on the wing or wings with DecoColor® paint pens, and released. (For 36 of these, I checked the underside of the hindwing for the small but conspicuous white marginal spots that are characteristic of E. tristis (Bailowitz & Brock, 1991); in all 36 cases, the spots were clearly present.) All marked individuals were captured on their perches and were therefore assumed to be males (Shields 1967). When marked individuals were resighted, their location was noted. These records can be compared with those made by Shields (1967) on a Californian population of E. tristis, especially with respect to the existence of favored perching sites, the extent of site fidelity at hilltops, and the period over which known individuals returned to a particular hilltop.

In addition to records made in the spring of 2009, small numbers of males were observed on four days from 10 to 19 September 2009 at the ridgetop during roughly hour-long periods in mid-afternoon.

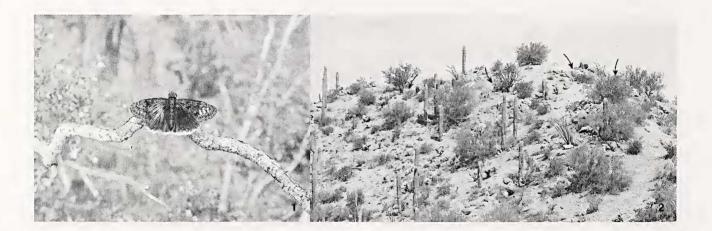
All means are presented ± 1 S.D.

RESULTS

During the spring study in 2009, presumptive males were found perched (Fig. 1) on plants growing near the ridgeline from as early as 1055 A.M. (Mountain Standard Time) to as late as 450 P.M. In the preceding four years, *E. tristis* was recorded as present from as early as 1000 A.M. to as late as 430 P.M.

While at the peaktop, males perched on a wide range of shrubs, trees, and cacti. The species chosen included jojoba (Simmondsia chinensis (Link) Schneider), creosote (*Larrea tridentata* (De Candolle) Coville), foothills paloverde (*Parkinsonia microphylla* (Torrey) Rose and I.M. Johnston), both living and dead buckhorn cactus (*Opuutia acanthocarpa* Engelmann & Bigelow), ocotillo (*Fouquieria splendens* Engelmann), and barrel cactus (*Ferocactus wislizenii* (Engelmann) Britton and Rose). One male also used a prominent boulder (about 1.5 m high) as his perch. Although the foodplants of *E. tristis* have been reported to be various species of oaks (Bailowitz & Brock, 1991), no species of *Quercus* has been recorded in the Usery Mountains to date (see http://swbiodiversity.org/seinet).

A total of twenty-three perch "sites" utilized by E. tristis were distributed along the 275 m census strip along the ridge that constitutes the top of Usery Mountain. A "site" was defined as an area of about 5 m in diameter containing from one to four nearby plants used by perching males. Seven of these sites were not located on the backbone of the ridge but were instead up to 8.5 m from the highest adjacent point on the ridge on the southfacing downslope (Fig. 2). Even those on the backbone of the ridge were often placed below nearby points of higher elevation. The mean distance between the generally well-spaced sites was 9.3 ± 8.8 m. Perching males were usually more than 10 m apart given that no more than 11 sites attracted a male on any one day during the study. The mean height of the perches themselves was 0.95 \pm 0.33 m for a sample (n=25) of one or two perches per site. Some marked individual males moved from one plant to another within or between sites during the observation period; others restricted themselves to one or a very few neighboring plants where they remained for at least 55 min in five cases.



Figures 1 and **2**. 1. A wing-marked male of *E. tristis* on a creosotebush in its territory in early March 2009. **2**. A portion of the ridge that constitutes Usery Peak. Perches used by territorial males of *E. tristis* are indicated by arrows. Note that these plants were not located on the highest adjacent portion of Usery Peak.

43: 1-5, 2010

Certain sites were far more likely to be occupied on any given day by a perching male than others. Over the 16 days of the study in 2009, three sites were occupied on at least 13 days; in contrast, seven sites were taken on just one or two days. The single most popular site in spring 2009 was also occupied in 2006, 2007 and 2008. During these three preceding years, plants in a total of 10 sites were recorded as being occupied by perching duskywings; eight of these were also utilized by perching males in the month long spring study in 2009.

When a male was present at his perch, he regularly launched flights of variable duration that took him out and around the shrub or tree before he returned (usually) to land on or near the spot where he had been prior to the flight. These flights occurred at a rate of 5.2 ± 1.8 per 5 min (n = 17 males observed on four days between March 15 and May 12, 2009). The vast majority (92%) of all recorded out and back flights (n=88) lasted less than 30 sec. In addition to apparently spontaneous flights, males also left their perches in pursuit of passing butterflies of their own and other species. When two male conspecifics interacted, the "resident" male usually chased after the "intruder" in a horizontal or gradually ascending flight that covered many meters. On other occasions (n=7), however, the two males quickly converted an ascending pursuit flight into a spinning descending flight in which the two individuals appeared to turn rapidly about one another at very close range. One male appeared to get above the other as the spinning pair descended until the lower butterfly was close to the ground, where it sometimes landed. At some point, the lower individual ended the interaction by flying rapidly away from the other male, which pursued the departing butterfly as it left.

Some of the males captured and marked on Usery Peak returned on one or more days subsequently. Of the 38 marked males, 15 (39%) were seen again on the peaktop on another day. The mean interval between first and last sighting for this sample was 8.5 \pm 5.7 days. Site-specific fidelity was not strong; all 15 returning males perched in more than one site during the time they were observed on the peak with a mean number of 2.5 \pm 0.6 sites taken. (The mean total number of days on which returning males were seen on the peaktop was only 2.9 \pm 0.9.) Thus, males were not strongly wedded to one perch or a few adjacent ones.

In 2009, hilltopping *E. tristis* were seen during five months from February through May, and again during September. In 2006, the species was seen on Usery Peak in August and October as well. Thus, the species appears to have two lengthy flight seasons at

this location separated by the very hot, dry months of June and July.

During the limited observations made in the midafternoon during September 2009, only a few males appeared. These individuals occupied a total of six sites, five of which had been occupied at least once during the spring study period. The most frequently taken territory in this brief fall study was the same one favored during the spring of the year. The site fidelity of males to their perches appeared to be very low, given that all attempts to watch perched individuals for 5 min each ended with the abandonment of the site by the observed male after a mean of 3.2 ± 1.0 min (n=6 males observed on three different days).

One mating pair was observed along the ridgetop in the afternoon of March 11, 2005.

The only congener of *E. tristis* seen on Usery Peak during the study was *Erynnis meridianus* Bell, 1927, which appeared on the hilltop on four days between 12 and 17 September 2009 between 1040 A.M. and 330 P.M. Three individuals were marked; one was seen on the day after marking at a site at the other end of the transect from where it had been captured and paint-marked on the wing. No more than three sites were held by this species during any one observation period of about an hour.

The behavior of *E. meridianus* was very similar to that of its congener. The males perched on shrubs growing along the ridge that constitutes Usery Peak. The plants chosen were a creosotebush, three different jojoba bushes, and dead staghorn cactus skeleton. The cactus skeleton had been frequently taken by *E. tristis* earlier in the year. Four individuals were watched for 5-min periods during which the presumptive males made no more than two flights out and back to their perch. Two of these flights were obviously triggered by a heterospecific butterfly flying near the perch. Two other cases of apparent male-male conspecific interactions took place, both involving ascending flights by the participants.

DISCUSSION

The mating system of *E. tristis* in central Arizona is very similar to that recorded for this same species in California (Shields 1967). Hilltopping males defend perches on plants from which vantage points they can presumably detect incoming females, although malefemale encounters were much less often seen at Usery Peak than at the Californian hilltops where Shields (1967) observed 18 mating pairs of *E. tristis*. While waiting for females, males in both locations perched for variable periods from the middle of the day to the late afternoon on exposed branches and twigs of

4 J. Res. Lepid.

shrubs. Shields (1967) recorded a maximum stay of 45 minutes; one male in the current study stayed at his site for at least 70 min. At both locations, some marked males returned to defend a perch or perches over a period of days. Returning males constituted only 11% of the sample in Shields (1967) study; at the Arizona site, resightings were considerably more common with returning males making up nearly 40% of the marked and released sample. Perhaps this difference derives from the fact that the Arizona hilltop was visited more often by an observer than the California hilltops. In keeping with this possibility, Shields (1967) recorded a maximum interval of four days between marking and resighting whereas three marked males at the Arizona site were seen from between 16 and 21 days after marking. Both the Arizona and California hilltops attracted perch-defending males year after year (for five consecutive years in Arizona and three years in the California study).

Shields (1967) noted that aggressive interactions with conspecifics were uncommon in the hilltopping E. tristis that he studied. He apparently did not observe the "spinning" descending male-male fights that occur on Usery Peak. These latter flights are highly convergent in form with the aerial interactions of the territorial tachinid fly Leschenaultia adusta (Loew 1872) (Alcock & Kemp, 2006). In both the butterfly and the fly, some males appear to be forced to the ground by their opponent. In contrast, males of many other hilltopping butterflies engage in elaborate ascending flights when challenged by a determined intruder. On these occasions, the two rivals spiral about one another as they fly more or less straight up into the sky. Sometimes, males of E. tristis also pursue intruders upwards but in a more gradual ascent that lacks the wing clashing element seen in species like the nymphalid Chlosyne californica (Wright, 1905) (Alcock, 1984) and various swallowtails (Rutowski et al., 1989).

Another difference between the behavior of *E. tristis* and some other hilltopping butterflies lies in its selection of landmark perches. Species like the hairstreak butterflies *Atlides halesus* (Cramer, 1777) (Alcock, 1983) and *Strymon melinns* (Hübner, 1818) (Alcock & O'Neill, 1986) launch their territorial flights from elevated perches in prominent foothill paloverdes and creosotebushes growing right on the backbone of the mountain ridge at its higher points. These same perching plants are used by a host of other hilltopping insects (e.g., Alcock, 1981; Alcock & Dodson, 2008). Many other hilltopping insects, ranging from the butterfly *C. californica* (Alcock, 1984) to various flies and wasps perch on the bare ground just a few meters from these prominent plants. In

contrast, *E. tristis* rarely perched in any paloverde and never did so in the taller trees and other plants atop the ridgeline. Instead, the skipper favored low shrubs or small skeletal staghorn cacti, which often were several meters downhill rather than on the backbone of the ridge.

Yet another difference between males of *E. tristis* and the plant-defending hairstreaks has to do with the site fidelity of territorial males. When a marked male of *S. melinus* was resighted, there was a nearly 80% chance that it would be found in the tree where it had been seen previously (Alcock & O'Neill, 1986). Likewise, prolonged occupation of a particular tree was commonplace in *A. halesus* with some individuals holding the same tree for periods in excess of a week (Alcock, 1983). Although many males of *E. tristis* were seen on more than one day on the peak, they regularly shifted from one perch site to another, even on the same day.

The distinctive behavior of E. tristis provides support for the observation of Rutowski (1991) that the various components of butterfly mating systems, such as perch site selection, site fidelity and contest behavior, can be considered separately in terms of their adaptive significance. This approach leads to a number of questions about the mating system of E. tristis that will require additional research. For example, do males of E. tristis use perching plants ignored by other species as a means of reducing the number of mistaken pursuits of other species, chases that require the expenditure of time and energy? Do males shift perch sites relatively frequently because arriving females are more evenly distributed along the ridgetop than are the females of most other hilltopping butterflies, and therefore males gain less by staying on perches in a very few of the most visually prominent landmark plants? And finally, why have males of *E. tristis* (and a few other hilltopping species) evolved descending flight contests when so many other hilltoppers exclusively engage in ascending spiral flights when in territorial disputes?

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